

Switching Between Cooperation and Competition in Social Selection

August Guang

Francis Su, Advisor

Stephen Adolph, Reader

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HARVEY MUDD
COLLEGE

Department of Mathematics

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Abstract

Joan Roughgarden proposed a theory called social selection as a behavioral game theoretic model for sexual reproduction that incorporates both competition and cooperation in 2006. (Roughgarden et al., 2006) Players oscillate between playing competitively to maximize their individual fitness, leading to a Nash Competitive Equilibrium, and playing cooperatively to maximize a team fitness function, leading to a Nash Bargaining Solution. Roughgarden et al. (2006) gives rates of change for both the competitive state and the cooperative state, but does not explain her rates or how to switch between the states in sufficient detail.

We test and rederive the rates, critiquing an assumption that the derivation of such a rate must make, as well as create a probabilistic model that switches between the two states. We test our model on the reproductive behaviors of *Symphodus tinca*, the peacock wrasse. The results follow the trajectory of the reproductive strategies for the wrasse throughout the breeding system, suggesting that cooperation could be a mechanism through which wrasse change their reproductive behaviors. However, the inputs to the model need to be analyzed more critically. Future work could include deriving rates for competitive play and cooperative play that do not rely on assumptions of being able to quantify strategy allocation proportion and refining the model and drawing generalized conclusions about it.

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Chapter 1

Introduction

In this chapter we explain social selection as a game theoretic model for sexual reproduction. We also give some game theory background on basic payoff matrices, competitive games, the Nash Equilibrium, noncompetitive games, and the Nash Bargaining Solution. We end by applying the Nash Equilibrium and the Nash Bargaining Solution to an example.

Joan Roughgarden describes possible mechanisms through which bargaining occurs in her model (Roughgarden et al., 2006). An explanation of Rubinstein's sequential bargaining model as another possible schema for the dynamics of bargaining is included in this chapter as well (1982).

1.1 What Is Social Selection?

Darwin's original theory of sexual selection proposed that sexual reproduction is a competitive game. Individuals of the same sex compete with each other for mates, and an individual of the opposite sex chooses the winner of the competition on the basis that that winner has more desirable genes.

There are many species that this theory does not model well. For example, oystercatchers are a type of bird that has threesomes guarding nests, usually two females and one male. The females might compete with each other, or they might work together to take care of the chicks and guard the nest.

Roughgarden et al. (2006) proposed an alternate theory to sexual selection called social selection, which is based on cooperative game theory. Players, which are individuals within a species, communicate with each other through threats and side payments. The payoff is "reproductive fitness".

She sets up a two-tier model, the first of which is the evolutionary tier and the second of which is a behavioral tier. At the evolutionary tier, natural selection prevails to increase the diversity and longevity of the entire species, and at the behavioral tier, individuals within a species cooperate and compete with each other to increase either their individual fitnesses or their team fitness. The behavioral tier is the one based on cooperative game theory.

A *cooperative game* is defined as a game in which communication is allowed and players can make binding agreements. A noncooperative or *competitive game* is one in which players seek to maximize their individual utility without communication. *Teams* are defined as groups of individuals that work towards a common goal. This is different from a *coalition*, which is a group of individuals who have coincident self-interests. Finally, the underlying motivation behind players choosing to play the game cooperatively is “pleasure”, based on empirical observations according to Roughgarden et al. (2006). Animals will arrive at a Nash Bargaining Solution through maximizing a common objective function through pleasure-based teamwork.

Social selection is hence a two-tier theory where individuals switch between cooperative and competitive behavior in order to maximize reproductive fitness so that the diversity and longevity of the species is increased.

1.2 Background: Game Theory

We can think of game theory as the mathematical theory of decision-making. Each *game* has a set of players who choose between a set of strategies. Based on the *strategies* these players choose, they end up with different *payoffs*. Players act to maximize these payoffs.

In biological interactions, players are individual animals, while payoffs would be the fitness conferred upon these animals. One can think of fitness as likelihood of survival, or survival of offspring.

The payoffs and strategies for a two player, n -strategy game can easily be visualized by a *payoff matrix*. The one below is an example from Straffin (1996), which will be used later on as well.

The payoffs are the entries of the matrix. These payoffs are represented in pairs, where the first value in the pair is the payoff to Player 1, and the second value in the pair is the payoff to Player 2.

In a competitive game, a win for one player is a loss for the other. An important concept in competitive game theory is that of the *Nash Equilib-*

| | | Player 2 | |
|----------|---|----------|---------|
| | | A | B |
| Player 1 | A | (2, 6) | (10, 5) |
| | B | (4, 8) | (0, 0) |

Table 1.1 Straffin two-by-two matrix.

| | | Player 2 | |
|----------|---|----------|--------|
| | | A | B |
| Player 1 | A | (2, 6) | (6, 9) |
| | B | (4, 8) | (0, 0) |

Table 1.2 Bargaining two-by-two matrix.

rium. A Nash Equilibrium is a pair of strategies that gives neither player an incentive to deviate. In other words, two players are at a Nash Equilibrium if neither player can do better by switching their chosen strategy.

In Table 1.1, there exists a Nash Equilibrium when Player 1 plays *B* and Player 2 plays *A* for a payoff of (4, 8). If Player 1 switches to strategy *A* while Player 2 remains at *A*, then their payoff will decrease to 2. If Player 2 switches to strategy *B* while Player 2 remains at *B*, then their payoff will decrease to 0. Hence, neither player can do better by switching their chosen strategy.

1.3 Nash Bargaining

If players are able to communicate and make agreements, then the Nash Equilibrium may not be as good of a solution concept. Perhaps players can bargain and make side payments to reach a more optimal solution. For example, with Table 1.1, if players could bargain, then Player 1 might notice that they could increase their payoff if they could induce Player 2 to play strategy *B* while they played strategy *A*. To accomplish this, they might offer Player 2 a side payment of 4 to play strategy *B*. In this case, the new payoff matrix would be:

We see that in this new payoff matrix there are at least *two* Nash Equilibria, (Player 1-A, Player 2-B) and (Player 1-B, Player 2-A). (Player 1-B, Player 2-A) is the Nash equilibrium from the example above. For (Player 1-A, Player 2-B), we see that if Player 1 switches to strategy *B* then their payoff will decrease to 0, and if Player 2 switches to strategy *A* then their pay-

off will decrease to 2. However, the two Nash Equilibria are not the same: (Player 1-A, Player 2-B) yields a higher payoff than (Player 1-B, Player 2-A).

In any game, players can play *mixed strategies* by partitioning time into playing certain strategies to maximize their individual payoffs. For example, if we imagine that Table 1.1 is a repeated game, then Player 1 could play strategy *A* 40% of the time, and strategy *B* the other 60% of the time. Assuming Player 2 plays strategy *A*, Player 1 gets a payoff of

$$0.4 \times 2 + 0.6 \times 4 = 0.08 + 0.24 = 0.32,$$

and assuming Player 2 plays strategy *B*, Player 1 gets a payoff of

$$0.4 \times 10 + 0.6 \times 0 = 0.4.$$

Nash came up with a solution concept called the *Nash Bargaining Solution* to determine how players should make these partitions in a cooperative game.

First we explain how bargaining is modeled. Suppose two players are bargaining over something. Then there exists a set of outcomes S that their bargaining might attain. This set S is called the *bargaining set*. Each player i has a utility scale u_i that ranks the outcomes that they prefer. The players bargain to try to get the most preferable outcome for themselves.

There exists an outcome d_1 for player 1 and d_2 for player 2 that are their least preferable outcomes on their respective utility scales. The point (d_1, d_2) is the *threat point*, that is the outcome in the event that players are unable to reach an agreement.

Nash made four assumptions about the nature of the bargaining solution called the Nash Bargaining Axioms. If these four axioms are satisfied, then there exists a unique solution to the bargaining problem. Let $f(d, S)$ represent a solution to the bargaining problem where S is the bargaining set and d is the threat point.

Axiom 1: Invariance to Affine Transformations. A solution is invariant to affine transformations of utilities. In other words, a player's preference doesn't change based on the scale. If Player 1 prefers outcome x to outcome y , then they will always prefer outcome x to outcome y no matter what scale is used. Hence the solution should not be affected by an affine transformation in the utilities.

Mathematically, this says that if $T_1 : \mathbb{R}^2 \rightarrow \mathbb{R}^2$ is an affine linear transformation

$$T_1(x, y) = (ax + b, y),$$

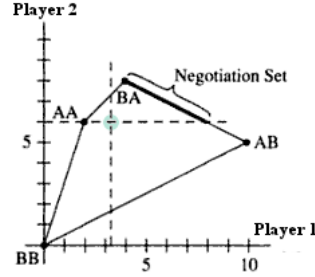


Figure 1.1 Payoff polygon for the game. Threat point is the light blue dot. Taken from Straffin (1996) and modified.

then

$$T_1(f(d, S)) = f(T_1(d), T_1(S)).$$

Axiom 2: Pareto Optimality. There should not be a solution that yields a better outcome for both players.

Axiom 3: Symmetry. If the set of outcomes S is symmetric with respect to the main diagonal and if $d_1 = d_2$, then the solution should assign equal utilities to both players.

Axiom 4: Independence of Irrelevant Alternatives. If a solution $s = f(T, d)$ is found in a set of outcomes T , then any subset $S \subset T$ containing s should still have s as the solution. In other words, the presence other alternatives are irrelevant to the solution.

Mathematically, this says that if $S \subset T$ and $f(T, d) \in S$, then $f(T, d) = f(S, d)$.

If Axiom 2 is satisfied, then the solution must exist along a set to the upper right of the threat point, known as the *negotiation set*:

It is known that the Nash bargaining solution is the unique point on that maximizes the product

$$(x - d_1)(y - d_2)$$

where $(x, y) \in S, x \geq d_1, y \geq d_2$.

1.4 Nash Bargaining Dynamics

The Nash Bargaining Solution provides a very useful concept for the solution two players will reach, but it does not explain the dynamics of how

players might arrive at the solution. It is known as a *static solution*. Roughgarden proposed a possible schema for the evolutionary dynamics of social selection, which we analyze in the following sections. Two other authors, Rubinstein and Binmore, have also worked extensively on bargaining dynamics in economics (Rubinstein, 1982; Binmore et al., 1986), and the following is an overview of their work.

1.4.1 Rubinstein's Strategic Bargaining Model

Suppose there are two individuals who would like to divide up a pie of size 1. Each makes a proposal at discrete time intervals as to how the pie should be divided sequentially. Then if player 1 gets x of the pie player 2 will get $1 - x$ of the pie. Furthermore, time is valuable to the players, so that as time increases the player has more incentive to make a deal. The preferences of each player are also continuous and stationary, or,

1. A player's preferences can be written as a lottery between that player's most extreme preferences, and
2. The preference of (x, t) over $(y, t + 1)$ if x and y are outcomes and t is time is independent of t .

Rubinstein seeks to answer the question of what agreement will be if both parties behave rationally.

Two more conditions can be added for two different sub-families of models:

- Fixed bargaining cost: Player i 's preference is given by the function $y - c_i t$ where c_i is a constant, so every player has a fixed cost for each bargaining step.
- Fixed discounting factor: Player i 's preference is given by the function $y\delta_i^t$ where δ_i is a constant, so every player has a proportional discount for each bargaining step.

A final assumption is that the players have complete information about the preferences of the others.

The main thrust of the paper is that a Nash equilibrium is inadequate as a way to decide how the pie will be partitioned, as every possible partition is a Nash equilibrium. Hence the author defines a Perfect Equilibrium Partition (PEP) as a unique solution; a PEP is a pair of strategies such that the player who has to continue the bargaining has no better strategy than

to follow the planned strategy. In other words, a PEP is a pair of strategies such that if a player plans to accept an offer, then they have no better alternative than to accept the offer, and if a player plans to reject an offer, then they have no better alternative than to reject the offer. There exists a unique PEP for most cases.

The outcomes are as follows. With fixed bargaining cost,

1. If $c_1 > c_2$, the PEP is that player 1 gets c_2 of the pie.
2. If $c_1 = c_2$, then any partition of the pie where player 1 gets at least c_1 , or any partition x such that $c_1 \leq x \leq 1$ is a perfect equilibrium partition. In other words, player 1 cannot do better than getting c_1 of the pie, and player 2 cannot do worse than getting $1 - c_1$ of the pie.
3. If $c_1 < c_2$, then player 1 gets all of the pie.

With the fixed discounting factor model, if one of the δ_i is strictly less than 1, and if at least one of the δ_i is strictly positive, then the player who starts the bargaining gets $\frac{1-\delta_2}{1-\delta_1\delta_2}$. This solution is continuous and monotonic in the discounting factors, and the player who starts the bargaining gets the relative advantage.

1.4.2 Strategic Bargaining Solution Approximates Nash Bargaining Solutions

Binmore et al. (1986) attempted to clarify how Rubinstein's strategic bargaining model and the Nash bargaining solution were related. In a two-person bargaining situation, the set X represents possible agreements, and $x \in X$ represents the payoffs for each player. There are also utility functions for both players, rating either their attitudes towards risk or their attitudes towards time, as well as certain conditions relating to the bargaining procedure (who makes the first offer and at what times?) and environment (can the process be interrupted by random events?).

The authors deal with two basic motives that would lead to bargaining rather than competition. The first is the players' desire to maximize their individual payoffs in minimal time, and the second is their desire to avoid the consequences of not reaching agreement. One can think of it as the desire to not minimize their individual payoffs.

Static problems are without consideration for how the offers are made. This paper elaborates on the strategic model used in Rubinstein (1982) by incorporating the two motives to get two different models, then showing

that the Nash bargaining solution approximates the perfect equilibrium in each model. However, the two motives lead to different agreements with respect to the underlying set X of physical consequences to the two parties, as the utility functions are different.

For a description of the strategic bargaining model, see the Rubinstein commentary.

The conclusion is that if the bargaining situation is different then the Nash bargaining solution is still valid given that the model is set up correctly. This involves careful construction of the set S of utility functions, the set s^0 of the threat point, the symmetry axiom, and addition of other assumptions.

1.4.3 Time Preference

We look at the strategic bargaining model where the players value time in reaching agreement. Suppose two players are trying to divide up a pie of size 1. Let

$$X = \{(x_1, x_2) | x_1, x_2 \geq 0, x_1 + x_2 \leq 1\}$$

represent the set of possible agreements for dividing up this pie. Then x_1 is the proportion of pie player 1 gets and x_2 is the proportion of pie player 2 gets. Let d be the outcome when the players never reach an agreement. Bargaining is made at discrete time intervals $0, \Delta, 2\Delta, 3\Delta, \dots$ where Δ is the length of a single bargaining period.

Let an agreement be defined as (x, t) , where x is a partition of the pie (so $x \in X$) and $t = n\Delta$ is the time at which the agreement is reached. Let $A \equiv_i B$ mean that player i is indifferent between A and B . Furthermore, assume that there are time-indifferent agreements, or there exists $g \in X$ and $\tau = n\Delta$ such that $(g, \tau) \equiv_i (g, 0)$ (the set X must be large enough to have such an agreement). Additional assumptions are,

- Stationarity. If $(x, \tau) \geq_i (y, \tau + v)$, then $(x, \tau') \geq_i (y, \tau' + v)$.
- Monotonicity in time. If $\tau < \tau'$ then $(x, \tau) >_i (x, \tau')$.
- Continuity. A player's preferences can be written as a lottery between that player's most extreme preferences.
- Concavity of compensation. Both players are risk-averse.

Then from Rubinstein (1982), there exists $x^*, y^* \in X$ such that $(x^*, \Delta) \equiv_1 (y^*, 0)$ and $(y^*, \Delta) \equiv_2 (x^*, 0)$. If both players prefer x^* and y^* to g and d ,

then there is a unique perfect equilibrium - player 1 refuses anything below y^* and always demands x^* and player 2 refuses anything above x^* and always demands y^* .

If player 1 starts then the equilibrium outcome is $(x^*, 0)$ and if player 2 starts then it is $(y^*, 0)$.

Chapter 2

Roughgarden's Model

In this chapter we give an overview of the model Roughgarden et al. (2006) developed for social selection. We describe the specific parameters, variables, and rates in her model, as well as where it draws from game theory. We end up with an application of her model to an example.

2.1 The Model

In Roughgarden's model, time is a variable (Roughgarden et al., 2006). Proportions of time are spent playing strategies, and are continually adjusted as players attempt to maximize either individual fitness or cooperative fitness.

Consider a two-player, two-strategy game. There exists a 2×2 payoff matrix for this game. Let $w_{ij,k}$ represent that payoff for Player k when Player 1 plays Strategy i and Player 2 plays Strategy j . As an example, consider the example from Straffin (1996) once again:

| | | Player 2 | |
|----------|---|----------|---------|
| | | A | B |
| Player 1 | A | (2, 6) | (10, 5) |
| | B | (4, 8) | (0, 0) |

In this case, $w_{AA,1} = 2$ and $w_{AA,2} = 6$.

In individual play, players play strategies that attempt to maximize their own individual fitness independent of the other players' fitness. Let $p_1(t), p_2(t)$ be the proportion of time player 1 and player 2 play strategy A, respectively. Then $1 - p_1(t)$ and $1 - p_2(t)$ is the proportion of time player

1 and player 2 play strategy B, respectively. Let $w_i(p_1, p_2)$ represent the expected individual fitness for player i given p_1, p_2 ; that is,

$$w_i(p_1, p_2) = p_1 p_2 w_{AA,i} + p_1 (1 - p_2) w_{AB,i} \\ + (1 - p_1) p_2 w_{BA,i} + (1 - p_1) (1 - p_2) w_{BB,i}.$$

The rate of change at which player i changes playing strategy A is similar to that for coevolution between two species:

$$\frac{dp_i}{dt} = \frac{1}{w_i(p_1, p_2)} \left(\frac{\partial w_i(p_1, p_2)}{\partial p_i} \right) \times p_i (1 - p_i).$$

Roughgarden et al. (2006) gave no other justification for the rate besides mentioning coevolution, and cited no other references. The intuition we developed is that the direction of the strategy change will depend on the partial of the fitness as the strategy changes. The rate of change will not be very large if the fitness at that point is very large already, and the rate of change will also not be very large if the strategy time allocations are near 0 or 1 because it will take a while for the individuals to adjust their strategy time allocation, similar to population genetics. However, this analogy to population genetics seems dubious, as these are individuals rather than populations. These rates are explored more rigorously in Chapter 3.

In team play, both players attempt to maximize team fitness, defined as the product of each player's individual fitness given the threat point. Let $x_{AA}, x_{AB}, x_{BA}, x_{BB}$ be the proportion of the time the players jointly play AA, AB, BA , and BB respectively, and let v_i be the threat point to player i . Then the individual expected fitness for player i is

$$w_i(x_{AA}, x_{AB}, x_{BA}, x_{BB}) = x_{AA}(w_{AA,i} - v_i) + x_{AB}(w_{AB,i} - v_i) \\ + x_{BA}(w_{BA,i} - v_i) + x_{BB}(w_{BB,i} - v_i). \quad (2.1)$$

The team fitness is hence

$$w_1(x_{AA}, x_{AB}, x_{BA}, x_{BB}) w_2(x_{AA}, x_{AB}, x_{BA}, x_{BB}).$$

The rate of change for a joint strategy x_{ij} (where $ij \in AA, AB, BA, BB$) is similar to that of evolution within a single species:

$$\frac{dx_{ij}}{dt} = \frac{1}{w_1(x_{AA}, x_{AB}, x_{BA}, x_{BB}) w_2(x_{AA}, x_{AB}, x_{BA}, x_{BB})} \\ \times \left\{ \frac{\partial^* [w_1(x_{AA}, x_{AB}, x_{BA}, x_{BB}) w_2(x_{AA}, x_{AB}, x_{BA}, x_{BB})]}{\partial^* x_{ij}} \right\} \\ \times x_{ij} (1 - x_{ij}).$$

| | | Bird 2 | |
|--------|--------|--------|---------|
| | | Forage | Guard |
| Bird 1 | Forage | (2, 6) | (10, 5) |
| | Guard | (4, 8) | (0, 0) |

Table 2.1 Bird matrix.

2.2 Example: Birds Raising Chicks

Recall the payoff matrix from Straffin (1996) used above. We will use it as an example and interpret it to be a biological game. Suppose we have two birds, Bird 1 and Bird 2 that are attempting to raise a nest of chicks together. They each have two strategies, either to forage for food or to guard the nest. This results in a payoff matrix of Table 2.1. If both birds guard the nest, then no one will get food, hence all of their offspring will die, resulting in the payoff of (0, 0). Otherwise, both birds will get different fitness payoffs in terms of what is pleasurable to them, which is dependent on offspring survival but also on their individual willingness to forage or guard. The Nash Equilibria are at (Guard, Forage) and (Forage, Guard). At those points, neither bird has an incentive to change strategies, because their fitnesses will drop accordingly.

Each bird might notice that they enjoy foraging more than guarding, and hence negotiate an arrangement to divide time foraging and guarding. This could be reached by threat point — Bird 1 could threaten to go forage as well if the current arrangement is (Guard, Forage), which would drop Bird 1's fitness but would also drop Bird 2's fitness, and Bird 2 could threaten to do the same if the current arrangement is (Forage, Guard).

The threat point is the payoff for both players that results in the best fitness each could achieve given that they play individually. In this case the threat point is $(\frac{10}{3}, 6)$. Based on this threat point one can draw the payoff polygon given in Figure 1.1.

Everything to the right of and above the dashed lines is hence a better payoff for both players than the threat point payoff. The negative slope line from BA to AB, to the upper right of the threat point and cut off at the dashed line, represents the Pareto-optimal payoff region, or the line on which no outcome exists that is better for both players, or better for one player and equal for the other player. This is called the negotiation set. The Nash Bargaining Solution will be found on this set as the point on the line

(x, y) which maximizes the product

$$(x - x_0)(y - y_0)$$

where (x_0, y_0) is the threat point. In this case, the point $(5.7, 7.2)$ is the Nash Bargaining Solution, corresponding to Bird 1 foraging $\frac{5}{18}$ of the time and Bird 2 foraging $\frac{13}{18}$ of the time, respectively.

This is an example of how animals could cooperate and maximize their payoffs using the Nash Bargaining Solution. It does not explain how they would arrive at a Bargaining Solution, or why a Bargaining Solution makes sense. Roughgarden hypothesizes that the Nash Bargaining Solution arises out of cooperating players trying to maximize their team fitness as defined above. This would make sense because the team fitness is defined as the product of the individual fitnesses subtracted by the threat points.

2.3 Conclusion

Roughgarden et al. (2006) hypothesizes cooperation through pleasure, and defines team fitness in a way that causes individuals to converge to a Nash Bargaining Solution rather in accordance with the axiomatic approach Nash developed. She gives no axiomatic derivation of the Nash Bargaining Solution in the biological context, nor does she explain the dynamics of how a team arrives at the Nash Bargaining Solution.

In the next few chapters, I plan to explore

1. The rates of change for the amount of time put into a strategy and whether they converge to a Nash Competitive Equilibrium or a Nash Bargaining Solution.
2. How individuals might switch between individual play and team play.

Chapter 3

Rates of Convergence

In this chapter we examine the rates of change Roughgarden et al. (2006) gives for individual play and team play. As no justification was given for the rates beyond stating analogies to coevolution of species, we first test the rates to verify the correctness, come up with other potential rates that also lead to the correct solutions, and finally rederive the rates by drawing from adaptive topography (Wright, 1932). We critique one of the assumptions that must be made in the derivation of the rates.

3.1 Motivation

Roughgarden et al. (2006) proposed rates of change for individual play and team play that would explain the evolutionary game dynamics of how a Nash Equilibrium would be reached in individual play and how a Nash Bargaining Solution would be reached in team play.

Recall the rates of change:

$$\begin{aligned}\frac{dp_i}{dt} &= \frac{1}{w_i(p_1, p_2)} \\ &\times \left\{ \frac{\partial w_i(p_1, p_2)}{\partial p_i} \right\} \\ &\times p_i(1 - p_i).\end{aligned}$$

$$\begin{aligned} \frac{dx_{ij}}{dt} = & \frac{1}{w_1(x_{AA}, x_{AB}, x_{BA}, x_{BB})w_2(x_{AA}, x_{AB}, x_{BA}, x_{BB})} \\ & \times \left\{ \frac{\partial^* [w_1(x_{AA}, x_{AB}, x_{BA}, x_{BB})w_2(x_{AA}, x_{AB}, x_{BA}, x_{BB})]}{\partial^* x_{ij}} \right\} \\ & \times x_{ij}(1 - x_{ij}). \end{aligned}$$

The motivation behind these are the coevolution of species and Fisher's Fundamental Theorem of Natural Selection. (Fisher, 1930) However, there is otherwise no justification of the motivation behind the rates of change in strategy partitioning, nor any proof of why they lead to the Nash Competitive Equilibrium or the Nash Bargaining Solution.

3.2 Testing Rates of Convergence

Since there was no justification of these rates, we first tested them. To do so, we simulated individual play and team play in Python.

We made four functions for both individual and team play. The first calculated the average fitness accumulation rate for individual i given p_1, p_2 and the payoff matrix W . The second calculated the rate of change for p_i or x_{ij} according to the formula above, given p_1, p_2 , the payoff matrix W , and a time step.

The main function of the script calculated the value the game converged to as well as the equilibrium (p_1, p_2) . Its inputs were the initial values of p_1, p_2 , the payoff matrix W , and the time step to be taken.

At discrete time intervals, the players would adjust the proportion of time they put into playing different strategies. This continued until the rate of change became 0; at this point their average fitnesses had converged.

The final function plotted the fitnesses to which the different values converged.

3.3 Individual Play

Individual play was simulated in Python. The rates of change lead fitnesses to converge to the Nash Competitive Equilibriums at very small steps, such as 0.0001 (Table 3.1). However, at larger time steps such as 0.1, the fitnesses did not converge to a Nash Competitive Equilibrium.

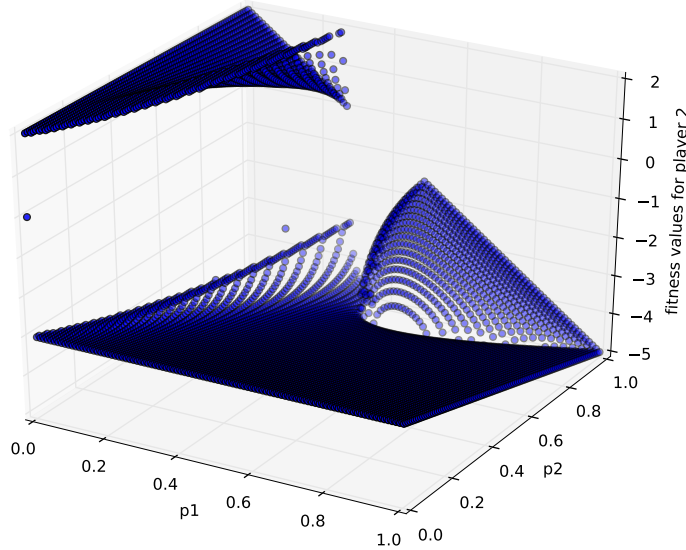


Figure 3.1 Individual play, converged average fitness accumulation rate, time step = 0.0001.

3.3.1 Given Rate

We entered the same payoff matrix as from Table 1.1, with starting values of p_1 and p_2 from 0 to 1 by 0.1 increments. We used a time step of 0.1. The converged fitness values are given in Figure 3.2.

We also tested a zero-sum payoff matrix, (a game where one player loses as much as the other gains) with a single Nash Equilibrium at $(3, -3)$, given in Table 3.1. The converged average fitness accumulation rates for Player 2 are given in Figure 3.3.

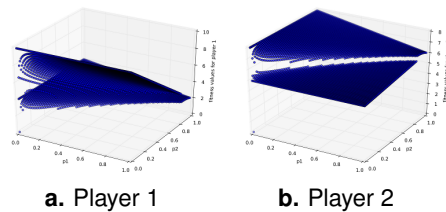


Figure 3.2 Converged average fitness accumulation rate, Straffin example.

| | A | B |
|---|---------|---------|
| A | (5, -5) | (3, -3) |
| B | (-2, 2) | (0, 0) |

Table 3.1 Zero-sum payoff matrix.

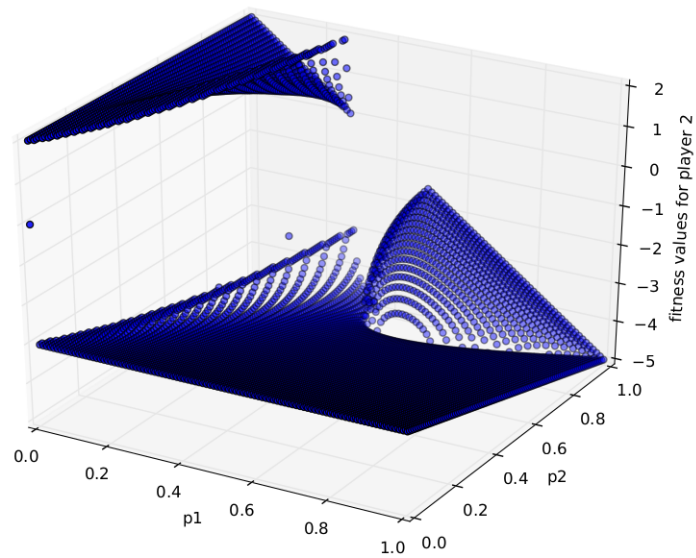


Figure 3.3 Converged average fitness accumulation rate for Player 2, zero sum.

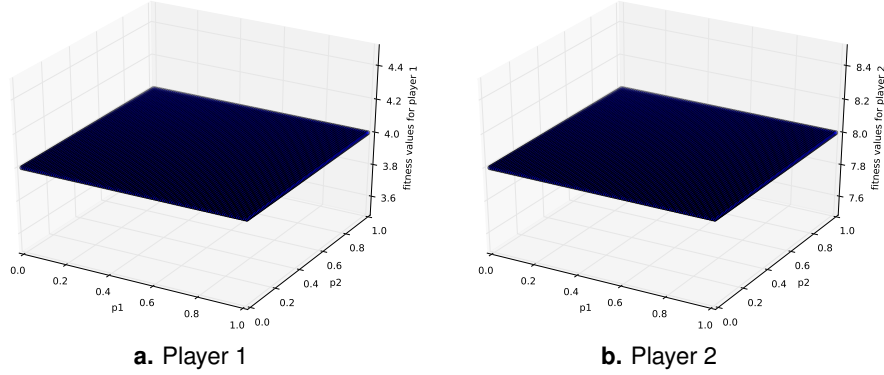


Figure 3.4 Converged average fitness accumulation rate, rate of change partial only, Straffin example.

3.3.2 Testing Other Rates

Originally, the rates of change Roughgarden gives did not lead to the Nash Equilibrium, as we were using time steps of 0.1. Since they did not converge, we tested two other possible rates of change with the payoff matrix from Table 1.1,

$$\frac{dp_i}{dt} = \frac{\partial w_i(p_1, p_2)}{\partial p_i}$$

and

$$\frac{dp_i}{dt} = \frac{1}{w_i(p_1, p_2)} \frac{\partial w_i(p_1, p_2)}{\partial p_i}.$$

We used the same starting values of p_1 and p_2 from 0 to 1 by 0.1 increments as above. We used the same time step of .1. The converged fitness values for only the partial are shown in Figure 3.4. Note that the average fitness accumulation rates converge to the Nash Equilibrium no matter what value of \mathbf{p} is used.

The converged fitness values for Player 1 for the partial multiplied by $\frac{1}{w_i(p_1, p_2)}$ are given in Figure 3.5. Note that the average fitness accumulation rates also converge to the Nash Equilibrium no matter what initial value of \mathbf{p} we start with.

It is clear that the average fitness accumulation rate converges to the Nash Equilibrium when the rate of change is both just the partial and when the rate of change is $\frac{1}{w_i(p_1, p_2)} \times \frac{\partial w_i(p_1, p_2)}{\partial p_i}$. This raises the question of why

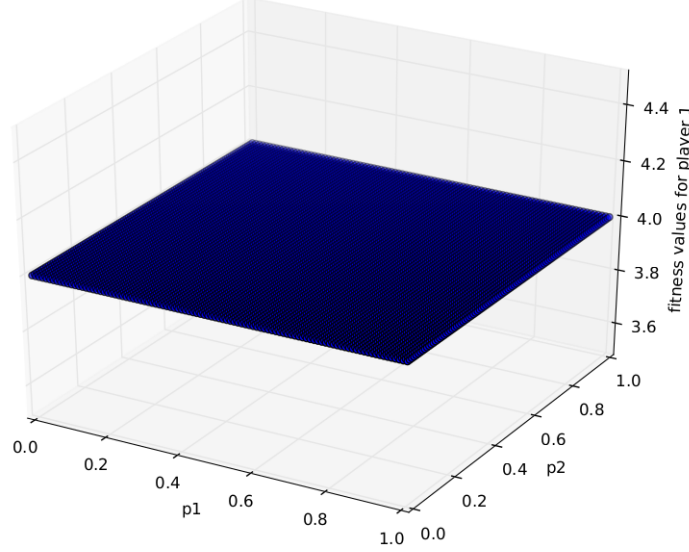


Figure 3.5 Converged average fitness accumulation rate, $(1/\text{Fit}) \times \text{Partial}$, Straffin example, Player 1.

Roughgarden chose to make use of the rate that she did rather than the partial or the partial divided by the average fitness.

3.4 Team Play

The code for team play has a few additional subtleties. First, the partial given for team play is a directional derivative that changes all the state variables in unison to maintain a total sum of one. In other words, as

$$\frac{\partial^* [w_1(x_{AA}, x_{AB}, x_{BA}, x_{BB}) w_2(x_{AA}, x_{AB}, x_{BA}, x_{BB})]}{\partial^* x_{ij}}$$

the three other state variables $x_{(1-i)j}$, $x_{i(1-j)}$, $x_{(1-i)(1-j)}$ change in the other direction as a block to preserve the total sum of 1.

In terms of modeling and simulation, we decided that the time allocations would be changed in proportion to the time allocation they already have. For example, if the rates were

$$x_{AA} = 0.4, x_{AB} = 0.2, x_{BA} = 0.1, x_{BB} = 0.3,$$

then if x_{AA} is changed by 0.1, then $x_{AB} = 0.2 - 0.1 \times (\frac{0.2}{0.6})$, $x_{BA} = 0.1 - 0.1 \times (\frac{0.1}{0.6})$, and $x_{BB} = 0.3 - 0.1 \times (\frac{0.3}{0.6})$. This block change would only occur and be added after all the rates for x_{ij} had been calculated.

After making the time step for the team play code 0.001 as well the team play rates led to the Nash Bargaining Solution. However, two things are of note:

1. The rate only works for those starting x_{ij} values that lead to positive average threat-point moderated fitnesses for both player, or starting values that cause the average fitness of the players to be above the threat point in the upper right corner of the payoff polygon.
2. If we take the absolute value of the term $\frac{1}{w_1 w_2}$ then we still achieve the Nash Bargaining Solution in some cases where the starting x_{ij} values do not give average fitnesses in the upper right corner of the payoff polygon, such as $x = [[0.2, 0.3], [0.4, 0.1]]$. However, in other cases the starting x_{ij} values do not converge to the Nash Bargaining Solution.

3.5 Derivation of Roughgarden's Individual Fitness Accumulation Equation

Roughgarden et al. (2006) claims that the individual fitness accumulation equations are analogous to coevolution of species:

“These equations resemble coevolution between two species, each with one haploid locus containing two alleles. Here, the notion of a ‘seconds pool’ replaces that of a gene pool, profitable seconds beget more profitable seconds with haploid inheritance, and the time-allocation variables change as each individual climbs their own adaptive surface, by analogy to the adaptive topography metaphor of population genetics.”

The key idea behind these equations is the Fundamental Theorem of Natural Selection, first explicated by Fisher (1930), then elaborated on by Price (1972). Modified versions of the theorem abound, as well as opinions about whether the theorem holds true or not. Nevertheless, Roughgarden adapts a version of this theorem to generate her fitness accumulation rate equations. We derive her individual rate below. The team rate has a similar derivation, but with a single species and four alleles instead.

We draw from adaptive topography for this derivation. Adaptive topography is a branch of evolutionary theory backed by the idea that natural

selection uses the genetic variation in a population to produce individuals that are adapted to the environment. In adaptive topography, the fundamental theorem of natural selection is

$$\Delta p = \frac{pq}{\bar{w}} \left(\frac{1}{2} \right) \frac{d\bar{w}}{dp}.$$

We will consider p_1 without loss of generality. Let $\bar{w} = W_i(p_1, p_2) = p_1 p_2 w_{AA} + p_1(1 - p_2)w_{AB} + (1 - p_1)p_2 w_{BA} + (1 - p_1)(1 - p_2)w_{BB}$. Then

$$\frac{\partial W_i(p_1, p_2)}{\partial p_1} = p_2 w_{AA} + (1 - p_2)w_{AB} - p_2 w_{BA} - (1 - p_2)w_{BB}.$$

Wright (1932) showed that if p is the frequency of the allele A and $q = 1 - p$ is the frequency of allele a in a haploid locus with two alleles, then

$$p_{t+1} = \left(\frac{p_t w_{AA} + q_t w_{AB}}{\bar{w}} \right) p_t,$$

so

$$\Delta p = p_{t+1} - p_t = \left(\frac{p_t w_{AA} + q_t w_{AB}}{\bar{w}} \right) p_t - p_t.$$

This derivation stems from the fact that the frequency of A alleles in the population at $t + 1$ is the number of As in the gamete pool divided by the total number of gametes produced, which is equivalent to the frequency of A alleles in the population at time t multiplied by the respective genotype fitnesses divided by the total fitness. Unfortunately, we cannot quantify the frequency with which players play strategy A in such a manner.

However, we conjecture that similar to Wright's equation, the frequency with which player 1 plays strategy A at $t + 1$ will be the amount of fitness player 1 accumulates by playing strategy A over the total fitness accumulation:

$$p_{1,t+1} = \frac{p_{1,t} p_{2,t} w_{AA} + p_{1,t} (1 - p_{2,t}) w_{AB}}{\bar{w}}.$$

If this holds true, then

$$\begin{aligned} \Delta p_1 &= p_{1,t+1} - p_{1,t} \\ &= \left[\frac{p_{2,t} w_{AA} + (1 - p_{2,t}) w_{AB}}{W_i(p_1, p_2)} \right] p_{1,t} - p_{1,t} \\ &= \frac{p_{1,t}}{W_i(p_1, p_2)} \times [p_{2,t} w_{AA} + w_{AB} - p_{2,t} w_{AB} - p_{1,t} p_{2,t} w_{AA} \end{aligned}$$

$$\begin{aligned}
& -p_{1,t}(1-p_{2,t})w_{AB} - (1-p_{1,t})p_{2,t}w_{BA} - (1-p_{1,t})(1-p_{2,t})w_{BB}] \\
& = \frac{p_{1,t}}{W_i(p_1, p_2)} [w_{AA}(1-p_{1,t})p_{2,t} + w_{AB}(1-p_{1,t})(1-p_{2,t}) \\
& \quad - (1-p_{1,t})p_{2,t}w_{BA} - (1-p_{1,t})(1-p_{2,t})w_{BB}] \\
& = \frac{p_1(1-p_1)}{W_i(p_1, p_2)} [p_2w_{AA} + (1-p_2)w_{AB} - p_2w_{BA} - (1-p_2)w_{BB}].
\end{aligned}$$

Note that the term on the end is exactly the partial derivative of $W_i(p_1, p_2)$ with respect to p_1 . Hence our equation becomes:

$$\Delta p_1 = \frac{p_1(1-p_1)}{W_i(p_1, p_2)} \frac{\partial W_i(p_1, p_2)}{\partial p_1}.$$

3.6 Questions and Criticisms

Other rates of change lead to a Nash Equilibrium, such as just the partial of the average fitness ($\frac{\partial W}{\partial p_i}$) or the partial divided by the average fitness. Other rates of change also lead to a Nash Bargaining Solution. The question then is: why the particular rate that Roughgarden has chosen to give? What is the justification for it?

While the rate she gives is analogous to coevolution between two species, it seems questionable that we can make such an analogy to individual general fitness from gametic fitness. Although both are driven by natural selection, one is quantifiable in the number of alleles produced, while the other is not. How can this anomaly be resolved? Would it make more sense to understand these rates and fitnesses as acting on populations? What would be the relationship between individual behavior and population behavior?

In addition, is it sensible for the team play rate to only work for those strategy time allocations that fall in the upper right side of the polygon? Could it not be conceivable that the team starts playing somewhere else in the polygon, and learn to play the Nash Bargaining Solution as well?

Finally, how do individuals switch between competition and cooperation? We explore this question in the next chapter.

Chapter 4

Switching Between Individual Play and Team Play

In this chapter we try to understand how players switch between individual and team play. Roughgarden cites a series of papers on hybrid system theory as a framework for the dynamics of switching between individual play and team play (see Tomlin et al., 2003). Hybrid system theory is the modeling, analysis and control of systems interacting between discrete and continuous state dynamics. An example of this would be airplane autopilot modes: a pilot would want to switch between discrete modes of autopilot controls based on continuous feedback. Hybrid system theory can be applied to social selection because individuals will switch between team play and individual play based on continuous rates of change in strategy time allocation. However, no such model as applied to social selection has been given, and hybrid system theory does not explain evolution between discrete states such as individual play and team play.

We develop a model for switching between team play and individual play. Another model that is influenced by Tomlin et al. (2003) is described in Chapter 5; there are technical coding problems with the model that have not made it testable yet. We also address the assumptions made in this particular model and its limitations along with possible future directions.

4.1 Probabilistic Model

Suppose two players play as a team $a\%$ of the time, and as individuals $1 - a\%$ of the time. When their style of playing improves upon their fitness,

they increment the proportion of time they play that style by a variable **chgAmt**.

4.1.1 Assumptions

- Playing as a team only requires one player realizing they can achieve a better fitness as a result of playing as a team. This is because that player can use the threat point to get the other individual to cooperate.
- When we had playing as a team require that both players decide to play cooperatively as opposed to only a single player, players always ended up playing competitively the entire time by the end. The idea was that it should be harder to get two individuals to agree on a set of strategies than for each of them to make their own choices, but it did not lead to interesting results, as in the payoff matrix we used it was never advantageous for Player 2 to cooperate.
- Players retain knowledge of the fitness benefits they accrued from the last time step.

4.1.2 The Pseudocode

Given a vector **p** that represents the proportion of time players 1 and 2 play strategy *A*, a 2×2 matrix **x** that represents the proportion of time the team jointly plays *AA*, *AB*, *BA*, *BB*, a fitness matrix **W**, a time step, and an initial proportion of time players play cooperatively *a*, and some constant change amount *b*, the pseudocode

```
for each time step up to t=100000:  
    choose team play with prob = a,  
        individual play with prob = 1 - a  
    change a by chgAmt according to whether style of  
        playing improves either player's fitness or not  
    if a becomes either 0 or 1: break
```

4.2 Results

We ran the code with a fixed **x** and fixed **chgAmt** while varying **p** and the initial team play proportion. For **x**, we fixed it at the Nash Equilibrium,

| | | |
|---------------------|--------------------|---------------------|
| 0 0 | 0 $\frac{5}{18}$ | 0.2 0.3 |
| 1 0 | $\frac{13}{18}$ 0 | 0.5 0 |
| a. Nash Equilibrium | b. Nash Bargaining | c. Additional Point |

Table 4.1 Specific x values used for analysis.

| | | Player 2 | |
|----------|---|----------|---------|
| | | A | B |
| Player 1 | A | (2, 6) | (10, 5) |
| | B | (4, 8) | (0, 0) |

Table 4.2 Straffin two-by-two matrix (Straffin, 1996).

Nash Bargaining Solution, and a random point in the payoff polygon that was not on the boundary. The three x values tried are in Table 4.1.

For **chgAmt**, we fixed it at 0.1, 0.01, 0.001, and 0.0001. Our fitness matrix was Table 1.1.

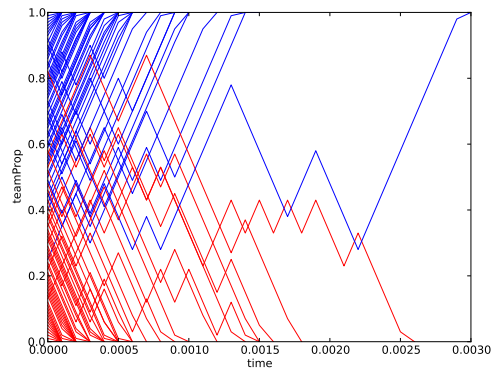
We include two kinds of graphs here for each of the three x s. One was varying \mathbf{p} by 0.1 (for both players, as in $\mathbf{p} = [0.1, 0.1]$, $\mathbf{p} = [0.2, 0.2]$, etc.) and varying the initial starting team play proportion by 0.1, and plotting the final team play proportion (Figures 4.2 and 4.5). This was not done for all values of **chgAmt** and x , as the purpose was mostly to see whether there was a middle region for the final team play proportion after ten time steps that did not converge to all competitive play or all team play.

The other was plotting the trajectory of the proportion of time players played as a team as time went on, with $p = [0.5, 0.5]$ and $p = [x_{AA} + x_{AB}, x_{AA} + x_{BA}]$, or the aggregate of the proportion of time each player was playing strategy A in x (Figures 4.1 and 4.6). Some graphs only feature $p = [0.5, 0.5]$ or p as the aggregate, as there did not seem to be significant differences in team play proportion trajectories based on p . This is not surprising, given that p remains independent from cooperative play dynamics.

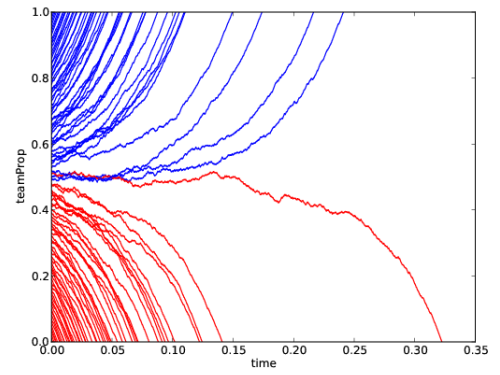
4.2.1 Nash Equilibrium

The team proportion always converged very quickly to either 1, all team play, or 0, all competitive play. The range where it was not clear whether team play would converge to 1 or 0 became smaller and smaller as **chgAmt** got smaller as well (Figure 4.1).

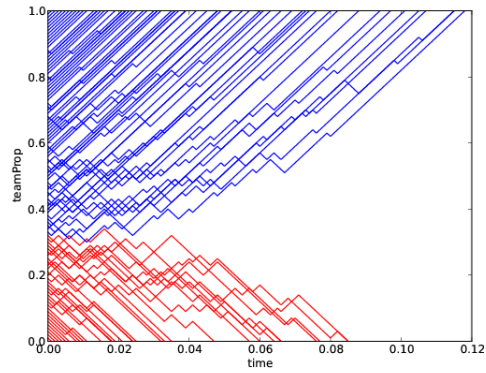
When we varied \mathbf{p} by 0.1 (for both players, as in $\mathbf{p} = [0.1, 0.1]$, $\mathbf{p} =$



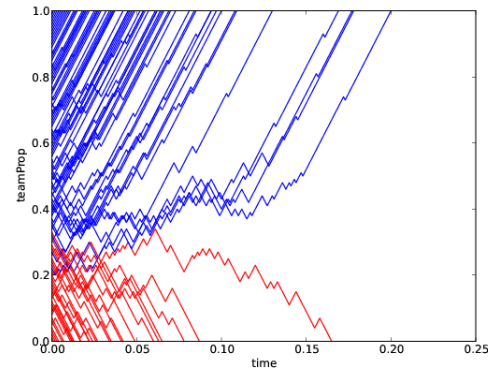
a. $p=\text{aggregate}$, $\text{chgAmt} = 0.1$



b. $p=\text{aggregate}$, $\text{chgAmt}=0.001$



c. $p=(0.5, 0.5)$, $\text{chgAmt}=0.01$



d. $p=\text{aggregate}$, $\text{chgAmt}=0.01$

Figure 4.1 Time vs. teamProp, Nash Equilibrium.

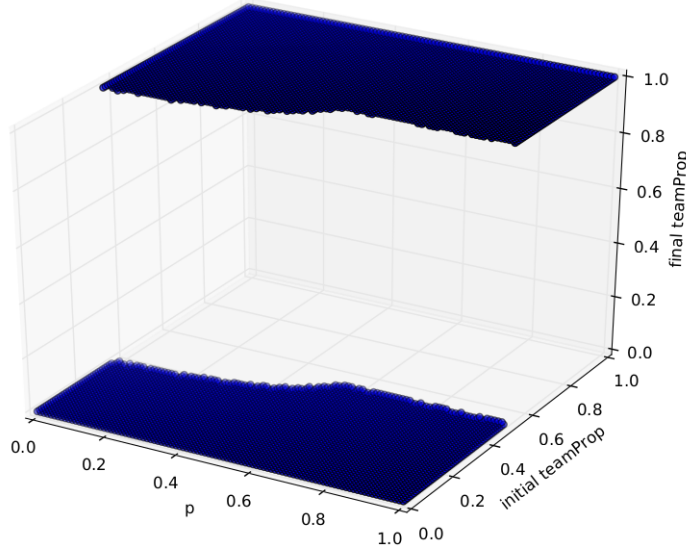


Figure 4.2 p , initial teamProp vs. final teamProp, $\text{chgAmt}=0.0001$, Nash Equilibrium.

[0.2,0.2], etc.) and varied the initial starting team play proportion by 0.1, we discovered that below ~ 0.45 players ended up playing competitively the entire time, and above ~ 0.45 players ended up playing cooperatively all the time (Figure 4.2).

4.2.2 Nash Bargaining Solution

The team proportion converged very quickly to 1, all team play, or 0, all competitive play for $\text{chgAmt} < 0.0001$. (Figure 4.3a) For $\text{chgAmt} = 0.0001$, there was a narrow window between 0.4 and 0.5 where it wasn't clear whether there would be convergence or not (Figure 4.3b).

When we plotted the trajectory of the team play proportion against time, we saw the same results: for $\text{chgAmt} < 0.0001$, the team play proportion converged to 0 or 1 quickly, and for $\text{chgAmt} = 0.0001$, there was a window between 0.4 and 0.5 where there was no clear convergence (Figure 4.4).

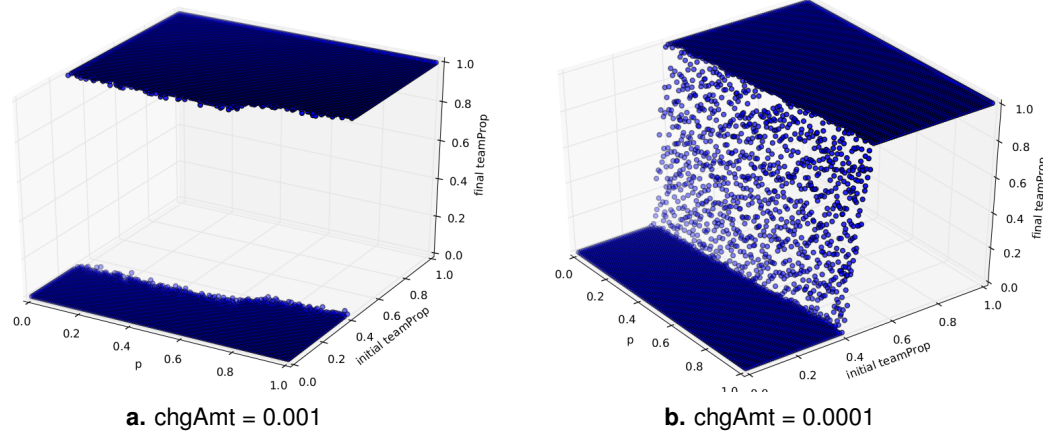


Figure 4.3 Initial teamProp vs. final teamProp, x = Nash Bargaining Solution.

4.2.3 Additional Point in Payoff Polygon

Here we tested different **ChgAmts** for the same point in the payoff polygon, $x = [[0.2, 0.3], [0.5, 0.1]]$.

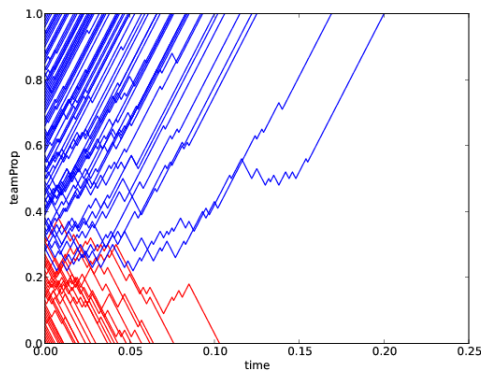
ChgAmt = 0.01

When we varied \mathbf{p} by 0.1 (for both players, as in $\mathbf{p} = [0.1, 0.1]$, $\mathbf{p} = [0.2, 0.2]$, etc.) and varied the initial starting team play proportion by 0.1, we discovered that below ~ 0.35 players ended up playing competitively the entire time, and above ~ 0.35 players ended up playing cooperatively all the time (Figure 4.5).

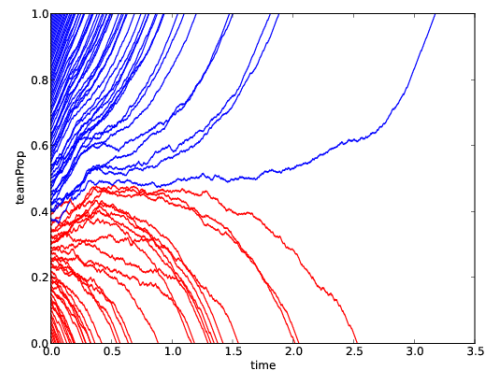
That same divide is reflected in the plots of the trajectory of the proportion of time players played as a team as time went on, with $p = [0.5, 0.5]$ and $p = [x_{AA} + x_{AB}, x_{AA} + x_{BA}]$, or the aggregate of the proportion of time each player was playing strategy A in x (Figure 4.6).

ChgAmt = 0.0001

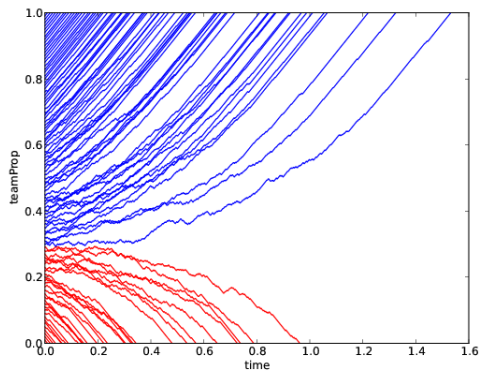
For **ChgAmt** = 0.0001, when we varied \mathbf{p} by 0.1 we discovered that there was a narrow window between 0.4 and 0.5 where the final team play proportion was not either 0 or 1, that if the initial starting team play proportion was less than 0.4 the players ended up playing competitively the entire



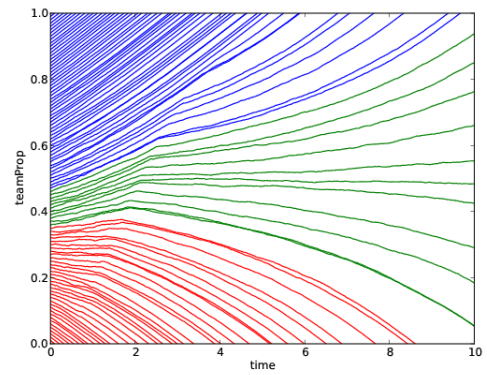
a. $p=(0.5, 0.5)$, $\text{chgAmt} = 0.01$



b. $p=\text{aggregate}$, $\text{chgAmt}=0.001$



c. $p=(0.5, 0.5)$, $\text{chgAmt}=0.001$



d. $p=(0.5, 0.5)$, $\text{chgAmt}=0.0001$

Figure 4.4 Time vs. teamProp, Nash Bargaining.

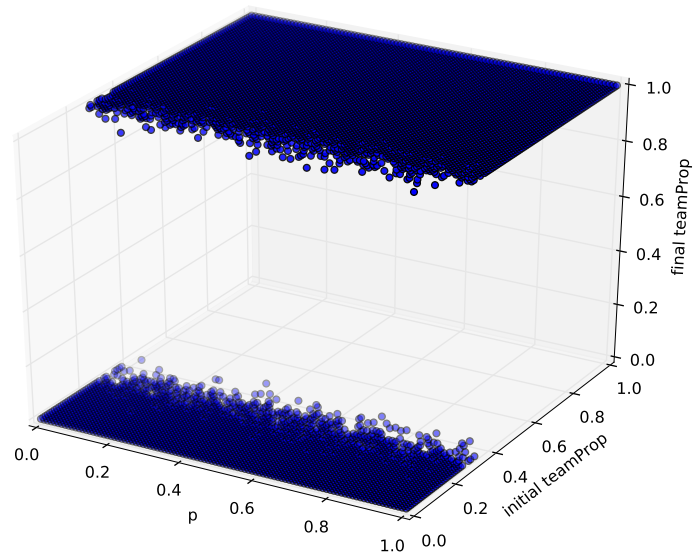
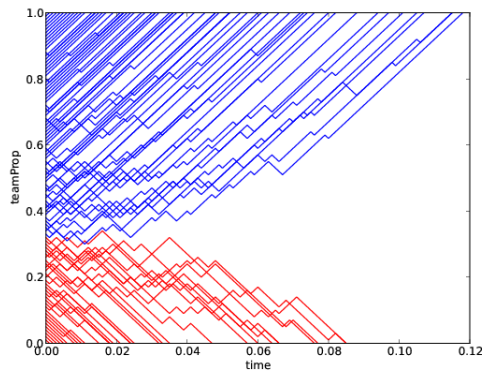
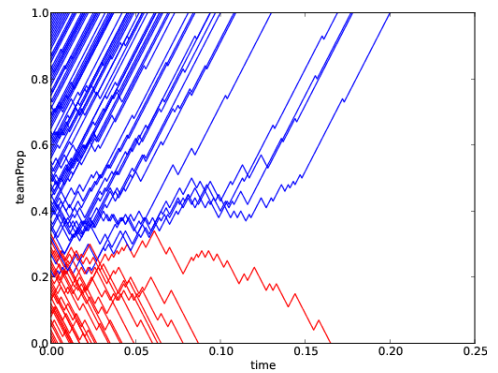


Figure 4.5 p , initial teamProp vs. final teamProp, chgAmt=0.1.



a. $p=(0.5, 0.5)$



b. $p=\text{aggregate}$

Figure 4.6 Time vs. teamProp, chgAmt = 0.01.

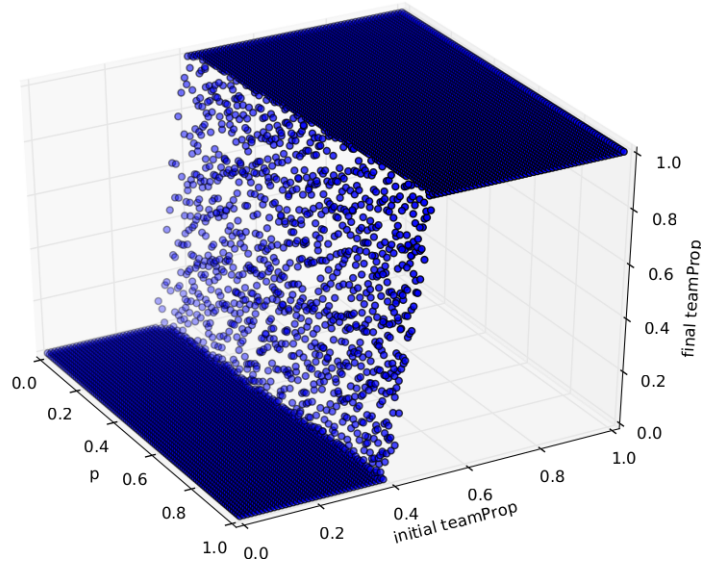


Figure 4.7 p , initial teamProp vs. final teamProp, chgAmt = 0.0001.

time, and if it was greater than 0.5 the players ended up playing cooperatively the entire time (Figure 4.7).

When we plotted the trajectory of the proportion of time players played as a team as time went on, we discovered the same thing (Figure 4.8). If the initial team proportion was less than 0.3, then players played competitively the entire time. If the initial team proportion was greater than 0.5, then players played cooperatively the entire time. At 0.4 it was not clear whether the play would converge or not, even after 100,000 adjustments. There was also a curious kink for the trajectory of team play proportion if the initial team play proportion was at 0.5, 0.4, or 0.3 that is not present in other starting proportions of team play. It remains to be seen as to why that is.

4.2.4 Limitations

- The adjustment of playing styles should not change by a fixed amount; that seems erroneous, and also the probability of players ever playing other strategy styles becomes extinguished.
- The proportion of time players play strategies A and B in individual play and jointly AA , AB , BA , BB in team play should inform each

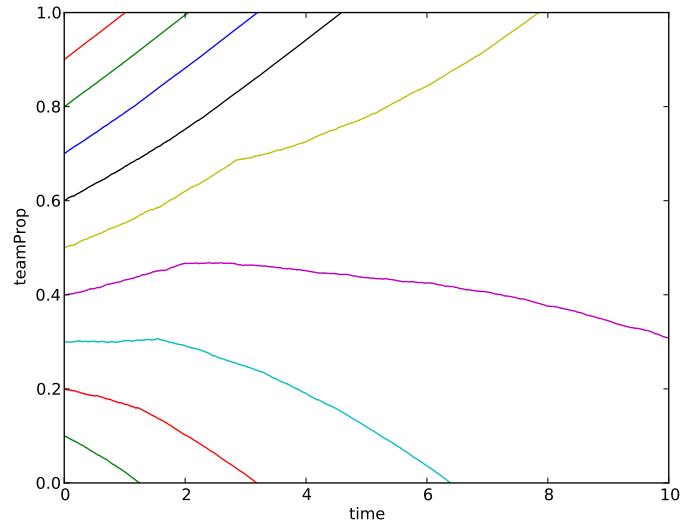


Figure 4.8 Time vs. teamProp, chgAmt = 0.0001, steps=100,000.

other. It is not likely that these are completely independent of each other.

- The decision as to when the proportion of time allocated to certain strategies was adjusted was made arbitrarily.

4.2.5 Possible Expansions

- Allow \mathbf{p} to depend on \mathbf{x} in some way.
- Allow some “trust” factor into play, where players are less likely to trust each other after having played competitively for a long time, and so the amount they adjust their likelihood to play as a team (such as **chgAmt**) by is proportionally lower.

4.3 General Directions

In the future, it would be interesting to allow \mathbf{p} to be based off of \mathbf{x} and vice versa. This is what has been done in the hybrid model described in Chapter 5, but no simulation has been done with it. Afterwards, incorporating some “trust” factor would be a simple change, given that we already have

chgAmt set up for the amount one moves towards cooperation or competition. In a different direction, looking at multichoice or fuzzy games (games in which there are levels between cooperation, cooperating partially, and not cooperating at all), and considering the game as a population or with more than two players may yield worthwhile results.

Our model is applied in Chapter 6 to the Peacock Wrasse as a test of whether it could explain changes in breeding behaviors in the wrasse.

Chapter 5

Other Models

In this chapter we list two other models that we developed. The first did not reveal any new information, and the second would be interesting to explore in depth, but requires more debugging.

5.1 Multi-Armed Bandit

The multi-armed bandit is a problem in statistics, where a player has a choice between multiple options that each produce a reward with a different probability. The objective of the player is to maximize the rewards they earn through choosing between options. It was originally considered by Allied scientists in World War II. It was proposed as a possible alternative to the model above because the players got fixed permanently into playing competitively because its initial outcome did better than that of playing cooperatively, which is similar to the dilemma of the multi-armed bandit.

The epsilon-greedy strategy can approximate an optimal sequence: the player picks the option that gives them the better fitness with $1 - \epsilon$ probability, and the other option (or options) with ϵ probability. In our model, this means that players pick the playing style that gives them better fitness with $1 - \epsilon$ probability, and the other playing style with ϵ probability.

5.1.1 Results

We have not tested this model thoroughly; originally we tested this model with the constraint that both players had to benefit positively from team play in order to continue playing as a team. This led to the players playing competitively almost the entire time, with the exception of playing co-

operatively occasionally in accordance with ϵ . This model could perhaps be tested using the new constraint that only a single player has to benefit positively from team play in order to continue playing as a team.

5.1.2 Possible Expansions

The bandit model could be incorporated into the probabilistic model, where the adjustment happens as in the probabilistic model, but players can never play cooperatively or competitively all the time. Instead the adjustment could be bounded by ϵ , so that players cannot play cooperatively more than $1 - \epsilon$ or less than ϵ percent of the time. This was done, however it did not reveal anything new. This is likely due to the fact that in the bandit model the proportion of team play still hovers at either ϵ or $1 - \epsilon$; since ϵ is small, it is unlikely for the proportion of team play to deviate far from either ϵ or $1 - \epsilon$.

5.2 Hybrid Model

In hybrid system theory, there are models and analyses of systems interacting between discrete and continuous state dynamics (Tomlin et al., 2003). There exist different continuous systems, with the discrete controlling which continuous system was in effect. An example of this would be airplane autopilot modes: a pilot would want to switch between discrete modes of autopilot controls based on continuous feedback.

Hybrid system theory can be applied to social selection because individuals will switch between team play and individual play based on continuous rates of change in strategy time allocation. However,

Roughgarden et al. (2006) referenced hybrid system theory as a framework for the dynamics of switching between individual play and team play, because individuals will switch between team play and individual play based on continuous rates of change in strategy time allocation. However, no such model as applied to social selection has been given, and hybrid system theory does not explain evolution between discrete states such as individual play and team play. We hence come up with our own hybrid model for switching between team play and individual play; it is essentially the same as the model from Chapter 4, with one key difference.

In hybrid systems, the state variables between different continuous systems remain the same, hence a model that was based off of hybrid system theory would have as its key feature the maintenance of the same state vari-

ables for each discrete state. This would be reflected in having \mathbf{x} be based off of \mathbf{p} , and vice versa. Note that

$$p_1 = x_{AA} + x_{AB}, \text{ and } p_2 = x_{AA} + x_{BA}.$$

Unfortunately, we cannot derive \mathbf{x} from \mathbf{p} in the same way. For the purposes of implementing the hybrid model, we set the entries of \mathbf{x} as

$$\begin{aligned} x_{AA} &= p_1 \times p_2, \\ x_{AB} &= p_1 \times (1 - p_2), \\ x_{BA} &= (1 - p_1) \times p_2, \\ x_{BB} &= (1 - p_1) \times (1 - p_2). \end{aligned}$$

This was the only change implemented in the hybrid model that was different from Chapter 4; at each step, after either \mathbf{x} or \mathbf{p} was adjusted, the other state variable was adjusted as well.

Preliminary tests do not show a significant difference between the hybrid model and the model where \mathbf{x} and \mathbf{p} are independent of each other. However, this model has not been tested in a systematic way.

5.3 General Directions

While first priority is given to refining the model in Chapter 4, if ideas from alternative models are found to be more salient or realistic, or show significant differences from Chapter 4 then more consideration will be given to these other models. In the next chapter we focus on applying Chapter 4 to a real-world example.

Chapter 6

Peacock Wrasse Example

In this chapter we run our model and the hybrid model on data taken from studies on the peacock wrasse (*Symphodus tinca*) to see if our model could predict potential mechanisms of cooperation occurring in species. Peacock wrasse are a Mediterranean fish that have relatively well understood strategies for breeding and a distinct breeding season that can be modeled (Luttbeg and Warner, 1999; Pallaoro and Jardas, 2003; van den Berghe, 1990).

Female wrasse choose between spawning with nonnesting males in unprotected areas, or spawning with nesting males in protected nests. Males have more strategy choices, from defending nests, (nesting males) searching the sea floor for females to spawn with, (interceptors) gathering around the edge of a defended nest to rush in whenever females spawned in one, (satellites) or taking over actively spawning nests then abandoning it to the defending males (pirates) (van den Berghe, 1988). However, the two main and most common male strategies researchers tend to focus on are nesting males and interceptors (Gross and Sargent, 1985), and for the purposes of this example, we allow only those two strategies for the male as well.

6.1 Introduction

Although individual peacock wrasse mating strategies have been studied extensively, how parental care or certain nesting strategies develop over the course of a season is not as well understood. The typical breeding season for peacock wrasses is from mid-April to mid-June.

Female wrasse provide no care, simply laying their eggs each day of the breeding season on either the sea floor or in a nest guarded by a male. They are observed to visit nests attempting to find an acceptable nest; after



Figure 6.1 *Symphodus tinca* (peacock wrasse).

a certain period of time they seem to “give up” and spawn out-of-nest. The relative payoffs of the two spawning options for the female wrasse depend on the fraction of eggs that hatch when a female spawns with a nesting or nonnesting male, the probability of successfully finding a nesting male, and the costs for the female of searching. It appears to be more profitable to search for and spawn with nesting males early in the breeding season and less so after mid-season due to a decrease in the availability of nesting males and probabilities of hatching success. One hypothesis of how females make reproductive decisions is through adjusting their giving up times, which are affected by their estimates of the probability of successfully finding an acceptable nest. Researchers created a model based on this hypothesis, and found that wrasse that adjusted their probability estimates based on previous experiences were the most successful at reproducing, and spawned in nests in proportions most similar to observed.

Male wrasse either provide facultative care, watching over eggs in a nest of algae and keeping them safe from predators, or provide no care. Van den Berghe described the progression of a large proportion of wrasse from no care to full care over the course of a breeding season. It was not clear how evolution to full care from no care came about, whether it was due to seasonal changes in terms of costs of providing care, availability of spawning females, out-of-nest mortality increases, a combination, or something else.

6.2 Model

We use our model to see whether some mechanism of communication between wrasse could also lead to the evolution of in-nest spawning behaviors. The parameters the model requires are a payoff matrix, an initial matrix of the proportion of time players play strategies jointly, an initial matrix of the proportion of time players play strategies independently, and an initial probability of playing as a team.

We used six different payoff matrices to represent the different periods of the roughly 90-day season: 10 day, 25 day, 40 day, 55 day, 70 day, and 85 day. For each of these days, we set the proportion of team play as the probability that a female wrasse successfully finds a suitable nest.

The initial matrix of the proportion of time players play strategies jointly is informed by the proportion of females spawning in nests and the proportion of males spawning in nests. These values were taken to be the initial matrix of the proportion of time players play strategies independently; the initial matrix of the proportion of time players play strategies jointly was then extrapolated as

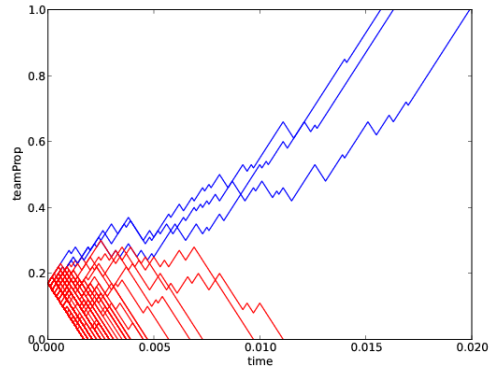
$$\begin{aligned}x_{AA} &= p_1 * p_2, \\x_{AB} &= p_1 * (1 - p_2), \\x_{BA} &= (1 - p_1) * p_2, \\x_{BB} &= (1 - p_1) * (1 - p_2).\end{aligned}$$

All of the initial parameters are in Table 6.1.

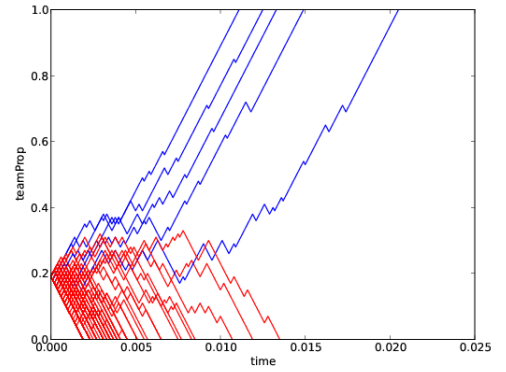
If only cooperation was in force, then the wrasse would all be spawning in nests. If only competition was in force, then two of the Nash equilibria are search-broadcast and stay-deposit; there may be others as well. However, as wrasse are observed to both spawn in nests and out of nests throughout the season, some other mechanism must exist that allows for multiple strategy pairs. We predict that our model will allow for wrasse to competitively play search-broadcast together near the beginning of the season, cooperatively and competitively play stay-deposit mid-season, and competitively play search-broadcast again near the end of the season.

6.3 Results

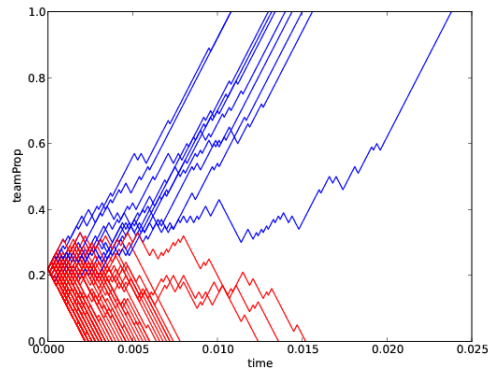
When we ran the models with the inputs listed in Table 6.1 we found that results were as expected. However, levels of cooperation were not high. The trends are shown in Figure 6.2.



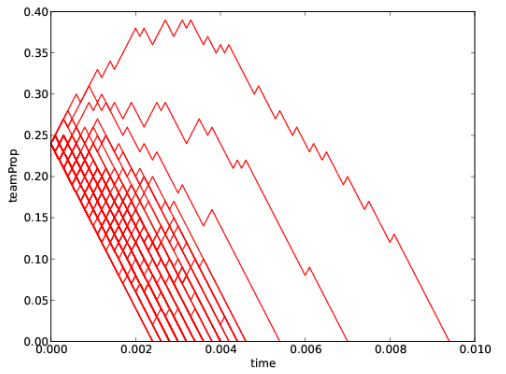
a. Day 10



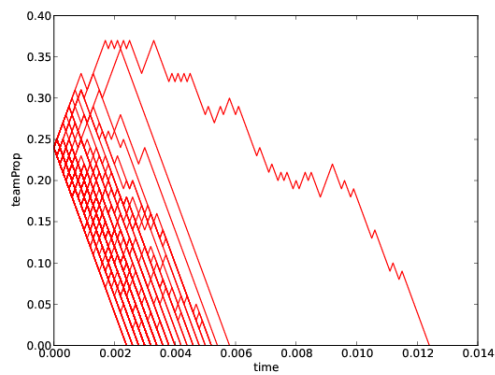
b. Day 25



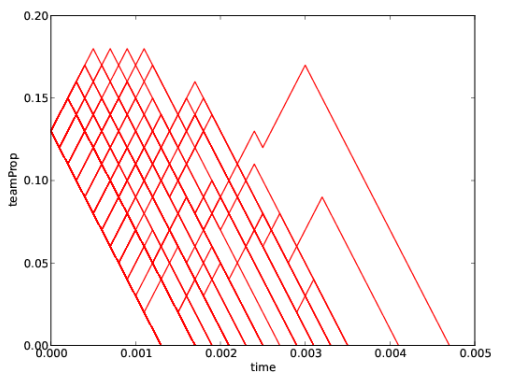
c. Day 40



d. Day 55



e. Day 70



f. Day 85

Figure 6.2 Progression of proportion of team play over season.

| Payoff Matrix | | x | | p | teamProp |
|---------------|------------|----------|-------|--------------|----------|
| (1, 1) | (0, 0) | 0.72 | 0.08 | [0.80, 0.90] | 0.17 |
| (0, 0) | (2.5, 2) | 0.18 | 0.02 | | |
| (1.5, 1.5) | (0, 0) | 0.50 | 0.30 | [0.80, 0.50] | 0.19 |
| (0, 0) | (4, 3.2) | 0 | 0.20 | | |
| (1.7, 1.7) | (0, 0) | 0.275 | 0.275 | [0.55, 0.50] | 0.22 |
| (0, 0) | (7, 5.6) | 0.225 | 0.225 | | |
| (3.5, 3.5) | (0, 0) | 0 | 0.25 | [0.25, 0] | 0.24 |
| (0, 0) | (9.5, 7.6) | 0 | 0.75 | | |
| (5, 5) | (0, 0) | 0 | 0.35 | [0.35, 0] | 0.24 |
| (0, 0) | (14, 11.2) | 0 | 0.65 | | |
| (4, 4) | (0, 0) | 1 | 0 | [1, 1] | 0.13 |
| (0, 0) | (14, 11.2) | 0 | 0 | | |

Table 6.1 Data Used For Wrasse.

6.4 Discussion

In our model, the wrasse develop from playing competitively search-broadcast to cooperatively playing stay-deposit and competitively playing search-broadcast, to competitively playing stay-deposit, and finally to competitively playing search-broadcast. This follows the general trajectory of breeding strategies for the male and female peacock wrasse, which suggests there may be mechanisms of cooperation and communication that act to cause peacock wrasse to switch strategies.

At Day 10, a small proportion of wrasse play cooperatively, leading to the stay-deposit pair of strategies, and a large proportion of wrasse play competitively, leading to the search-broadcast pair of strategies. At Day 25, a larger proportion of wrasse play cooperatively, leading to the stay-deposit pair of strategies, but the rest of the wrasse still play competitively, leading to the search-broadcast pair of strategies. At Day 40, the largest proportion of wrasse played cooperatively with stay-deposit; however the rest of the wrasse were also playing stay-deposit, but competitively.

Days 55, 70, and 85 were turning points, where wrasse were playing competitively the entire time, first at stay-deposit, then later at search-broadcast. One reason for the change from Day 40 to Day 55 could be that since all wrasse were playing stay-deposit at that point, there was no more

incentive to cooperate. As the season progressed, males stopped building nests, hence strategy play went to search-broadcast.

More research needs to go into what exactly are appropriate inputs and why, as well as understanding whether the model is an appropriate representation of wrasse breeding strategies throughout the season. In addition, while the model follows the general trajectory of breeding strategies, their initial inputs of \mathbf{x} and \mathbf{p} were already following the general trajectory of breeding strategies, hence the results of the model could simply be a reflection of the initial inputs. Finally, since the proportion of cooperation was so low, it cannot be concluded that cooperation is ever a significant mechanism leading to the strategy stay-deposit for the wrasse. In this particular model, since stay-deposit is a Nash Equilibrium as well as a Nash Bargaining Solution, the wrasse could have arrived at stay-deposit through competition as well. Perhaps a different model where the Nash Bargaining Solution is not the same as a Nash Equilibrium would be more revealing.

Chapter 7

Conclusions

Roughgarden's model of social selection hypothesized that evolution occurs on two tiers: one where selection acts on genes, and one where individuals change behaviors through mechanisms of competition and cooperation (2006). These mechanisms are rooted in game theory and ideas of the Nash Equilibrium and Nash Bargaining Solution.

Although Roughgarden et al. (2006) describes the rates of change for playing competitively and cooperatively, and our testing confirms that they correctly lead to the Nash Equilibrium and the Nash Bargaining Solution, they are not sufficiently justified. Although we have rederived the rates from Wright (1932), the derivation requires the assumption that strategy selection can be quantified in the same way that allele number can be quantified, which is not a reliable assumption to make.

Roughgarden et al. (2006) also does not describe how individuals would switch between playing competitively and playing cooperatively. We create a probabilistic model in Chapter 4 that would account for this switch and test it on *Symphodus tinca*, the peacock wrasse, breeding strategies using data from papers by Luttbeg and Warner (1999); Pallaoro and Jardas (2003); van den Berghe (1990). We also created other models using ideas from the multi-armed bandit and hybrid systems theory (Tomlin et al., 2003); these other models were not significantly different from the model from Chapter 4, so we did not pursue them further.

We expected the competition and cooperation proportions as well as strategies to change over the breeding season in a similar trajectory to that observed in the wrasse. While the model gave results that were in concordance with our predictions, the proportion of cooperation was very low, suggesting that cooperation may not be a significant mechanism in strat-

egy changes. In fact, because we changed the inputs to the model to reflect the seasonal changes in egg hatching probability and nesting availability, it could be possible that the model simply reflects the different inputs rather than predicts a similar trajectory of strategy changes.

Future work could include deriving rates for competitive play and cooperative play that do not rely on assumptions of being able to quantify strategy allocation proportion. The model could also use more refinement, with more generalized conclusions drawn. A deeper understanding of the model as well as the peacock wrasse would lead to a more conclusive understanding of whether the model can suggest cooperation and bargaining as a mechanism through which individuals within a species such as the wrasse switch behaviors, which is its ultimate goal.

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